

Additive effects of experimental climate change and land use on faunal contribution to litter decomposition

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ABSTRACT

Litter decomposition is a key process determining the cycling of nutrients in ecosystems. Soil fauna plays an essential role in this process, e.g., by fragmenting and burrowing surface litter material, and thereby enhancing microbial decomposition. However, soil fauna-mediated decomposition might be influenced by interacting factors of environmental changes. Here we used a large-scale global change field experiment to test potential interacting effects between land-use type (croplands and grasslands differing in management intensity) and projected climate change on litter decomposition rates over a period of two years. For that, climate and land-use treatments were orthogonally crossed: (1) two climate scenarios: ambient vs. future; and (2) five land-use regimes: conventional farming, organic farming, intensively used meadow, extensively used meadow, and extensively used pasture. Litterbags with two mesh sizes (5 mm and 0.02 mm) were used to differentiate contributions of microbes and fauna to the mass loss of standardized crop residues. Soil fauna accounted for more than 68% of surface litter mass loss. Future climate treatment decreased decomposition rates as a result of reduced precipitation and elevated temperature during summer months. Litter decomposition and the contribution of soil fauna to it were significantly higher in croplands than in grasslands, but did not differ due to management intensity within these land-use types. In grasslands, faunal contribution to decomposition decreased under future climate. There were no interacting effects between climate change and land use on decomposition rates. These findings indicate that predicted changes in precipitation patterns and temperature will consistently decelerate litter decomposition across land-used types via both microbial and faunal effects.

1. Introduction

Soil ecosystem functions are profoundly affected by anthropogenic climate and land-use changes (Mosier, 1998; Smith et al., 2016). Litter decomposition is one of the core biogeochemical processes, not only regulating the global carbon cycle and nutrient supply (Hättenschwiler et al., 2005; Stuart Chapin et al., 2012), but also corresponding to the community structure of soil biota and the dynamics of soil food webs (Cornwell et al., 2008; Gessner et al., 2010). To date, there is consensus that litter decomposition at the local scale is primarily regulated by abiotic factors (temperature and moisture; Gholz et al., 2000), litter traits (C, N and lignin; García-Palacios et al., 2016a) and soil organisms

(soil fauna and microflora; Gessner et al., 2010; García-Palacios et al., 2016b). At global scale, climate change and land-use intensification, as two major threats to biodiversity and ecosystem functioning, can be expected to mainly influence litter decomposition (Sala et al., 2000; Walter et al., 2013). However, very little is known about potential interacting effects of these main drivers of decomposition.

Soil fauna has a substantial influence on litter decomposition through the grazing activities on microbial communities, the physical breakdown and metabolism of organic material, which can modulate and pave the way for microbial decay (Bardgett and Wardle, 2010). Current climate change is mostly associated with warmer and drier soil conditions in many regions in the world (Dale et al., 2001; IPCC, 2014),

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which can influence soil biological processes, especially the activity of soil biota and litter decomposition (Hobbie, 1996; García-Palacios et al., 2013). In fact, a global decomposition experiment revealed that the effect of soil fauna on litter decomposition is climate-dependent (Wall et al., 2008). Likewise, a meta-analysis by García-Palacios et al. (2013) indicated that climatic conditions modulate the effect of soil fauna on decomposition in many biomes. Such climate change effects on litter decomposition are likely due to shifts in the structure and functioning of soil detritivore communities (Strickland et al., 2015).

In general, elevated temperature has often been shown to increase litter decomposition rates (Haugwitz et al., 2016; Hobbie, 1996) due to its stimulating effect on the faunal, microbial and enzymatic activities (Allison and Treseder, 2011; Liski et al., 2003; Luo et al., 2010). However, this effect is often offset under reduced water availability (Butenschoen et al., 2011; Gavazov, 2010), as soil moisture is main determinant and limitation of decomposition activities (Sanaullah et al., 2012; Vogel et al., 2013; Thakur et al., 2018). To date, however, there is no consensus on how exactly future climatic conditions will alter the structure and functioning of soil communities and how this will affect the provisioning of essential ecosystem services like litter decomposition. Moreover, it remains unclear if potential climate change effects on litter decomposition are consistent across different environmental contexts, such as different land-use regimes.

Soil functions are known to be influenced by many pressures from land-use type and management (Smith et al., 2016). Biodiversity and activity of soil microflora and fauna have been shown to suffer from the intensified land-use management (Mäder et al., 2008; Tsiafouli et al., 2015) and the conversion of land-use type, e.g., from grasslands to croplands (French et al., 2017). The abundance and diversity of soil fauna was found to decrease from meadows to croplands as well as with increasing management intensity within these land-use types (Ponge et al., 2013). Given the strong feedbacks between soil food webs and litter decomposition dynamics, land-use effects on litter decomposition via influences on the soil community are plausible. Thus, litter decomposition rates in general and the contribution of specific groups to this process can be expected to decrease with increasing management intensity. Accordingly, Castro-Huerta et al. (2015) demonstrated the relevance of management intensity in agricultural systems for how different groups of soil fauna influence decomposition dynamics. Due to the multitude of possible effects of both climate change and land use on litter decomposition, interacting effects of both global change drivers can be expected. There is, however, still a lack of experimental studies integrating these potential interacting effects.

Therefore, we conducted a split-plot design experiment with two climate scenarios, i.e., ambient vs. future; and five land-use regimes, i.e., (1) conventional farming – CF; (2) organic farming – OF; (3) intensively used meadow – IM; (4) extensively used meadow – EM; and (5) extensively used pasture (with sheep grazing) – EP, to estimate the potential interacting effects of climate and land use on litter decomposition as well as the role of soil fauna in this process. In detail, we addressed the following hypotheses:

1. Climate change characterized by summer drought will reduce microbial and faunal-driven litter decomposition rates. We expect to see the strongest climate change effects on litter decomposition with the combined effects of soil fauna and microbes.
2. Based on the assumption of higher activity of specific groups of soil biota in less intensively managed systems, we expect that litter decomposition rates are lower in croplands than in grasslands and decrease with more intensive land use within these two land-use types. This effect is especially strong in the presence of soil fauna.
3. Litter decomposition will be decreased by a synergistic effect of climate change and intensified land use, which is more pronounced in the presence of soil fauna.

2. Materials and methods

2.1. Study site

The experiment was conducted on the field site of the Global Change Experimental Facility (GCEF), which is a large experimental research platform located at the field research station of the Helmholtz-Centre for Environmental Research (<http://www.ufz.de/index.php?en=40038>). It was established on a former conventionally managed arable field (with the last crop in 2012) at Bad Lauchstädt, Saxony-Anhalt, Germany (51° 23' 30N, 11° 52' 49E, 116 m a.s.l.). Information on pesticide use before the establishment of the GCEF is not available. The soil is Chernozem with a high water storage capacity (31.2%) and storage density (1.35 g/cm³) (International Union of Soil Sciences Working Group WRB and Nations, 2006), as well as high nutrient contents (like N, P and K), which, together with a neutral pH value (~7.0), offers an ideal habitat for soil organisms (Altermann et al., 2005). The area is characterized by a sub-continental climate with a mean temperature of 8.9 °C and a low mean annual rainfall of 498 mm (long-term mean 1896–2013) resp. 9.8 °C and 516 mm (1995–2014). During the study period, the mean temperatures were 10.7 °C (2015) resp. 10.5 (2016) with an annual rainfall of 400 mm (2015) and 437 mm (2016).

2.2. Experimental set-up

The GCEF is composed of 10 main-plots with each main-plot consisting of five sub-plots (total 50 sub-plots) with a size of 24 m × 16 m. The five sub-plots within each main-plot are randomly assigned to the following five land-use regimes: (1) conventional farming; (2) organic farming; (3) intensively used meadow; (4) extensively used meadow; and (5) extensively used pasture (with sheep grazing) (for detailed description on all land-use regimes, see <http://www.ufz.de/index.php?en=40043>). The application of pesticides might be of relevance for litter decomposition studies. Notably, only the conventional farming treatment received several pesticides at the recommended agricultural rates during the study period (see Table S1). Half of the main-plots are subjected to ambient climate, the other half to conditions of a future climate scenario. This results in a split-plot design with climate as main-plot factor and land use as sub-plot factor (five replicates per climate × land use combination) with a minimum distance of 25 m among the main-plots.

Main-plots with future climate treatment are equipped with the steel construction (of 5.5 m height allowing the use of agricultural machines), mobile shelters, side panels and irrigation systems. This treatment is a consensus scenario across several models (REMO, Jacob and Podzun, 1997; RCAO, Döscher et al., 2002; COSMO-CLM, Rockel et al., 2008) of climate change in Central Germany for the years between 2070 and 2100. Shelters and panels automatically close from sundown to sunrise to increase night-time temperature (Beier et al., 2004), but cannot be operated in periods with strong frosts and high wind speed. The roof phases during our experiment were from February 15th to December 11th in 2015 and from March 22nd to November 29th in 2016. This night closing resulted in an increase of the daily mean of air temperature across the roof phases close to the ground (5 cm height) by 0.55 °C, in a depth of 1 cm by 0.62 °C, and in a depth of 15 cm by 0.50 °C. During the summer months (June to August), the roofs are additionally controlled by a rain sensor to decrease precipitation by ~20%. The irrigation system is used to increase precipitation in spring (March to May) and autumn (September to November) by ~10%. Main-plots with ambient climate treatment are equipped with the same steel construction, though without mobile shelters, side panels and irrigation systems, to avoid possible side effects of the construction itself and mimic possible microclimate effects of the experimental set-up.

Table 1

Results of repeated-measures split-split-plot-ANOVA of the effects of climate, land-use intensity (LUI, between the two cropland types and among the three grassland types, respectively), mesh size, period and their interactions on decomposition rates in (a) croplands and (b) grasslands. Significant effects ($P < 0.05$) are indicated in bold font.

Independent variables	a) Croplands			b) Grasslands		
	Df	F-value	P-value	Df	F-value	P-value
Climate	1:8	1.7	0.23	1:8	8.53	0.019
LUI	1:8	0.61	0.46	2:16	0.29	0.75
Climate × LUI	1:8	0.99	0.35	2:16	1.26	0.31
Mesh	1:16	275.14	< 0.001	1:24	412.33	< 0.001
Climate × Mesh	1:16	0.01	0.94	1:24	5.99	0.02
LUI × Mesh	1:16	0.25	0.67	2:24	0.94	0.4
Climate × LUI × Mesh	1:16	0.75	0.4	2:24	2.83	0.08
Period	5:40	97.18	< 0.001	6:48	361.55	< 0.001
Climate × Period	5:40	2.02	0.1	6:48	5.32	< 0.01
Land use × Period	5:40	1.54	0.2	12:96	1.29	0.24
Climate × LUI × Period	5:40	0.39	0.85	12:96	0.6	0.83
Mesh × Period	5:80	22.09	< 0.001	6:114	49.7	< 0.001
Climate × Mesh × Period	5:80	0.49	0.78	6:114	1.85	0.09
LUI × Mesh × Period	5:80	1.39	0.24	12:114	1.22	0.28
Climate × LUI × Mesh × Period	5:80	0.82	0.54	12:114	0.9	0.55

2.3. Litterbag study and experimental design

Decomposition rates were assessed using the litterbag method to estimate the contribution of soil fauna to litter mass loss (Seastedt, 1984). As a standard material, we used air-dried oat plants (with stems and leaves), which were harvested as green plants on the study site in 2013 before the start of the experiment. We filled 12 g into nylon litterbags (20 × 15 cm) with two different mesh sizes: (1) the fine-meshed litterbags with 0.02 mm mesh size allowed access of microbes (bacteria and fungi) and some microfauna (protozoans and nematodes); (2) the coarse-meshed litterbags with 5 mm mesh size additionally allowed access of macro- and mesofauna (Tian et al., 1992).

Within two years, litterbags were set in the fields during seven separate incubation periods: period 1 (spring): 10.04.2015–04.06.2015; period 2 (summer): 04.06.2015–10.08.2015; period 3 (winter): 22.10.2015–08.03.2016; period 4 (spring): 08.03.2016–07.06.2016; period 5 (summer): 28.06.2016–31.08.2016; period 6 (autumn): 31.08.2016–30.10.2016; period 7 (winter): 30.10.2016–07.03.2017. In each incubation period, a total of 200 litterbags (100 fine-meshed and 100 coarse-meshed) were placed into the 50 sub-plots. For this, we randomly placed two coarse-meshed and two fine-meshed bags per sub-plot along transect of 15 × 0.5 m. However, after the harvest of winter oat in the croplands in summer 2016, the respective sub-plots were treated weekly by soil cultivation procedures (stubble processing, ploughing) until sowing of subsequent crops. For this reason, it was not possible to place litterbags in croplands during period 5 in the sub-plots with conventional and organic farming (i.e., the present study is based on litter decomposition rates of 1320 litterbags in total). After retrieval of litterbags, soil particles, roots, and other non-target plant material adhering to remaining litter were removed. The cleaned litter residues were dried at 70 °C for at least three days to constant weight. Finally, the weight of the remaining litter was recorded to quantify the decomposition rates and soil faunal contribution.

2.4. Data analyses

We calculated litter decomposition rates (k) of each incubation period following the model derived by Olson (1963): $M_t/M_0 = e^{-kt}$. According to this equation, decomposition rates were calculated as $k = -\ln(M_t/M_0)/t$, with M_0 representing the initial dry mass of litter (g) and M_t the dry mass of the remaining litter after retrieving (g), and t as the number of days the litterbags were incubated in the field.

A repeated-measures ANOVA was conducted using a generalized linear mixed model (GLMM) with Type III sum of squares (procedure

MIXED, SAS University Edition v9.4) to analyze the decomposition rates in relation to the experimental treatments: in specific, the effect of climate (two levels) was analyzed at the main-plot level, the effect of land use (5 levels) and its interaction with climate at the sub-plot level, and the effect of mesh (2 levels) as well its interactions with the other two factors at the sub-sub-plot level. While these effects represented the between-subject model, the within-subject model considered the effect of period (repeated measure with 7 sampling events) as well as its interactions with the other experimental factors, again taking into account the split-split-plot design of the experiment. The factors main-plot (nested within climate) (i.e., the main-plot error) and sub-plot (nested within land use × climate) (i.e., the sub-plot error) were included as random terms. Since litterbags could not be established in the croplands during period 5, no direct comparison of land-use regimes across all periods was possible. Therefore, we conducted separate analyses for grasslands (including all periods) and croplands (without period 5). In addition, we performed a combined analysis for all land-use regimes excluding the results from period 5 for the grasslands. Here, we further calculated the linear contrast ‘croplands vs. grasslands’ to test our a-priori hypothesis that decomposition rates are lower in the two croplands compared to the three grasslands.

3. Results

Irrespective of the specific model, the decomposition rates were always significantly higher in coarse-meshed litterbags than in fine-meshed ones (Table 1a, b; Fig. 1a and b), and the contribution of soil fauna to litter mass loss was up to 68%–82% across land-use regimes (Fig. S1). In the model considering only the two cropland types (without data for period 5), the magnitude of this effect differed between the incubation periods (significant mesh × period interaction, Table 1a) with a stronger effect in the incubation periods 4 and 6 (spring and autumn of the second year, respectively, Fig. 1a) compared to the other periods. Similarly, the model examining the three grassland types showed largest differences between mesh sizes during summer (period 5) and autumn (period 7) of the second year (Fig. 1b).

The climate treatment did not significantly affect decomposition rates in croplands (Table 1a). On the contrary, the analyses of the three grassland types showed a significant effect of climate on decomposition rates (Table 1b). Under future climatic conditions, the decomposition rates were significantly lower compared to ambient climatic conditions, but only in coarse-meshed litterbags (Fig. 2a; significant climate × mesh, Table 1b). The effect of climate on litter decomposition in grasslands differed between periods (significant climate × period,

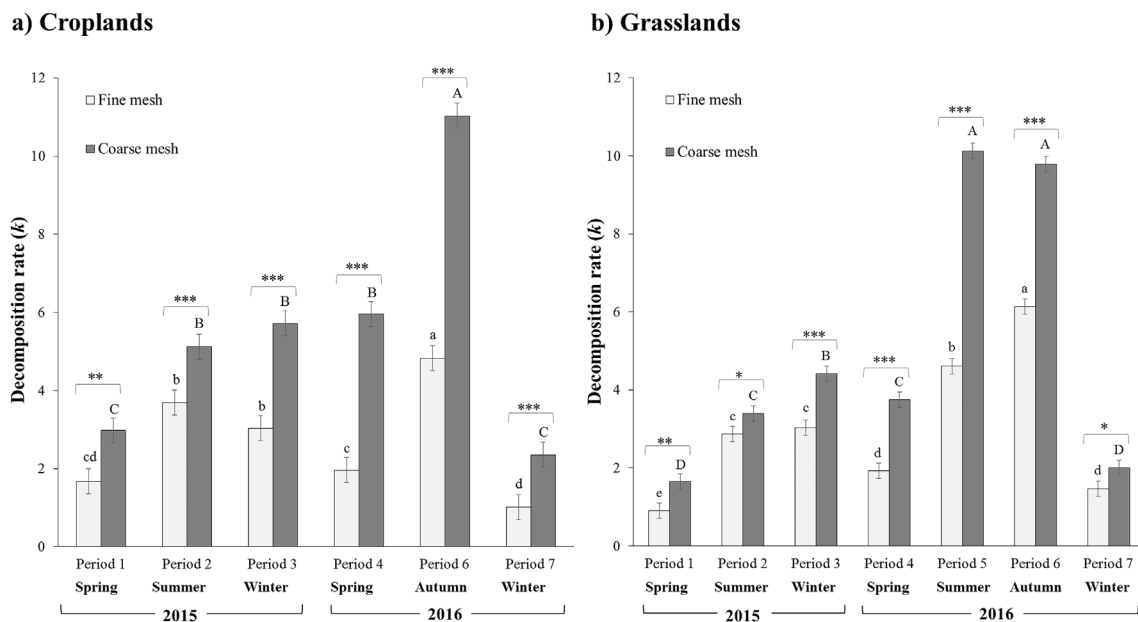


Fig. 1. Interacting effects of mesh size and period on the decomposition rate (k) in (a) **croplands** (CF and OF, without period 5) and (b) **grasslands** (IM, EM and EP). Notes: Given are means \pm standard error. Asterisks represent significant differences between the two mesh sizes within each period, with * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$. Different letters indicate significant differences following Tukeys HSD at $P < 0.05$ with separate comparisons indicated by lower- and upper-case letters, respectively.

Table 1b) with negative effects of future climate only occurring during the summer periods of both years (decomposition rates decreased by 36% in period 2 resp. by 14% in period 5, Fig. 2b). Land-use management intensity did not significantly affect decomposition rates within these two land-use types (croplands and grasslands, Table 1a, b).

From the model including the five land-use regimes without period 5 (summer 2016), we found significant land-use effects on decomposition rates, while only marginally significant climate effects and no interacting effects of both factors (Table S2). Further, this significant land-use effects resulted from a generally higher decomposition rates in

croplands than in grasslands (Fig. 3a; linear contrast ‘croplands vs. grasslands’: $F_{1,32} = 28.15$, $P < 0.001$, Fig. 3b). Decomposition rates were found consistently and significantly higher in coarse-meshed litterbags than in fine-meshed ones across the five land-use regimes. This effect was especially strong in the croplands (Fig. 3c). Further, we found that decomposition rates in coarse-meshed litterbags were significantly higher in croplands than in grasslands, whereas this rates in fine-meshed litterbags were extremely similar in both land-use types (linear contrasts ‘mesh x croplands vs. grasslands’: $F_{1,40} = 61.7$, $P < 0.001$, Fig. 3d). However, due to missing one most important period (period 5:

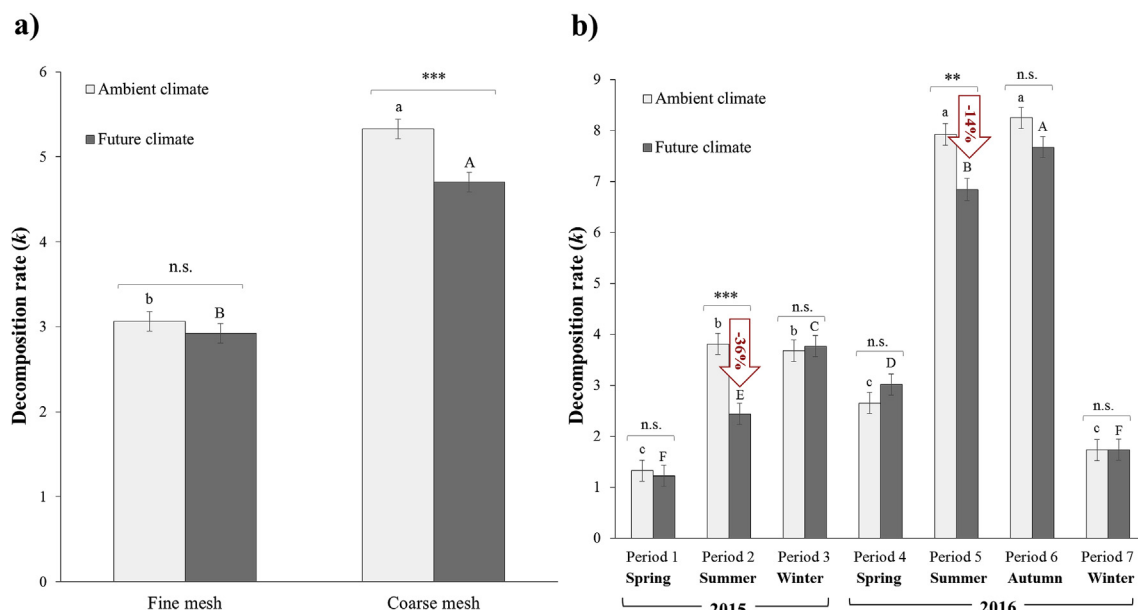


Fig. 2. Effects on decomposition rates in **grasslands** (IM, EM and EP): (a) Interacting effects of climate and mesh size on the decomposition rate (k) and (b) interacting effects of climate and period on the decomposition rate (k).

Notes: Given are means \pm standard error. n.s. represents non-significance, and asterisks represent significant differences between the two mesh sizes within each climate condition, with ** = $P < 0.01$, with *** = $P < 0.001$. Different letters indicate significant differences following Tukeys HSD at $P < 0.05$ with separate comparisons indicated by lower- and upper-case letters, respectively.

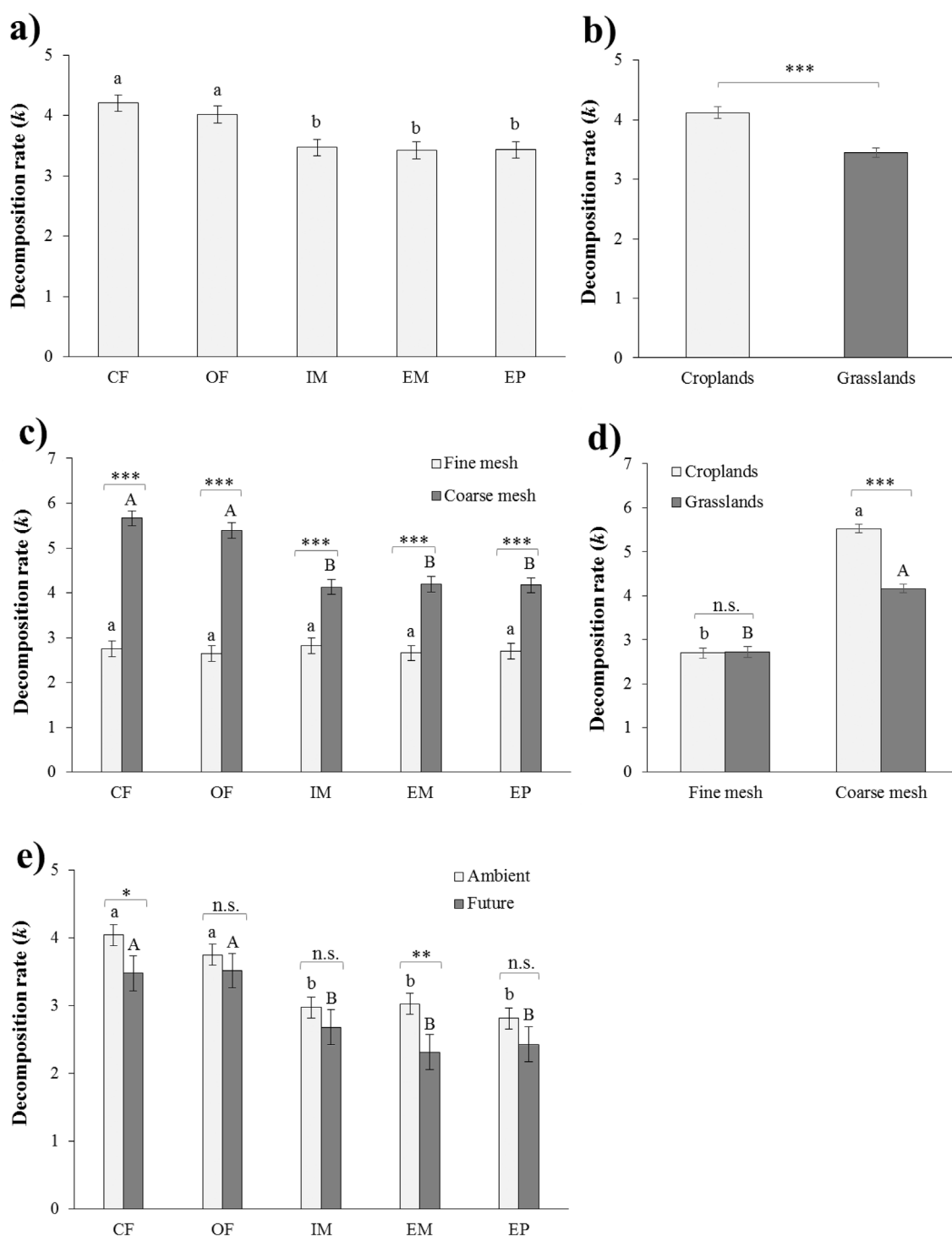


Fig. 3. (a) Effects of land use on decomposition rate with data from all land-use regimes without period 5. (b) Linear contrast 'croplands vs. grasslands' on the decomposition rate (k). (c) Interacting effects of land use and mesh size on the decomposition rate (k). (d) Linear contrast 'mesh x croplands vs. grasslands' on the decomposition rates (k). (e) Interacting effects of climate and land use on the decomposition rate (k).

Notes: Given are means \pm standard error. n.s. represents non-significance, and asterisks, in (b) represent significant differences between croplands and grasslands; in (c) represent significant differences between the two mesh sizes within each land-use regime; in (d) represent significant differences between the two land-use types within each mesh size; in (e) represent significant differences between the two climate treatments within each land-use regime, with * = $P < 0.05$, with ** = $P < 0.01$, with *** = $P < 0.001$. Different letters indicate significant differences following Tukey's HSD at $P < 0.05$ with separate comparisons indicated by lower- and upper-case letters, respectively. Abbreviations for land-use regimes: CF: conventional farming; OF: organic farming; IM: intensively used meadow; EM: extensively used meadow; EP: extensively used pasture.

summer 2016) in the second year, this result might underestimate the climate effect. Further, the climate treatment highly significantly interacted with the study period (Table S2), indicating temporary effects of climate. Accordingly, an analysis restricted to the first year (2015: period 1–3) yielded a significant climate effect on decomposition rates (Table S3). Moreover, a particularly strong negative effect of future climate could be demonstrated for the conventional farming and extensively used meadow (Fig. 3e).

4. Discussion

In accordance with our expectation, we found that predicted future climate decreased litter decomposition rates across grassland regimes. This effect was mainly due to a decelerated decomposition process during the summer months with reduced precipitation and higher temperature under future climatic conditions. The absence of this climate effect in the model considering only croplands was due to the fact that for technical reasons no decomposition data are available from the second summer period, where the significant climate effect in grasslands was observed. Accordingly, the significant climate effect was also found in croplands only considering the first year, indicating that there were no fundamental differences in the climate effect between croplands and grasslands. We therefore conclude that the reduced precipitation together with higher temperature in the summer months were the main drivers of the negative effects of the future climate scenario on litter decomposition dynamics. However, in our study summer and autumn were the seasons with the highest decomposition rates during the year, and negative effects of climate change were only evident for the summer periods. This highlights that higher soil temperatures will not favor litter decomposition, if the activity of soil organisms is limited by a low soil moisture in such periods (Gessner et al., 2010; Thakur et al., 2018). Any negative effects in such highly biologically active periods may have legacy effects and an important overall influence on communities and ecosystem processes (Tsiafouli et al., 2018). Accordingly, the effects of a slightly higher precipitation in spring and autumn and a slightly higher temperature throughout the growing season could not alleviate the overall negative effect of summer drought in our experiment. Vogel et al. (2013) also showed detrimental effects of summer drought on the decomposition rates of standard litter in experimental grasslands and explained this with reduced microbial processes. In our study, however, the negative effect of climate change on decomposition across the grassland types was only evident for litter with access to soil fauna.

In general, the activity of soil macro- and mesofauna accelerated the decomposition in crop- and grasslands considerably. Although the litterbag method is a commonly applied technique in decomposition studies, even the coarse mesh may restrict the access of potentially important decomposers like earthworms to a certain degree (Rhea-Fournier and Gonzalez, 2017). It should therefore be taken into account that any assessment of faunal contribution to litter decomposition using this method may rather be a conservative estimate of the real effect of soil fauna and thus more reliable.

Across the grassland types, the contribution of soil fauna to decomposition was higher under ambient climatic conditions, whilst microbial-driven decomposition alone was not affected by climate change. This indicates a key role of reduced faunal activity for the observed effects of summer drought on litter decomposition. Accordingly, climate is known to be an important modulator of the role of soil fauna to the decomposition process across spatial scales (García-Palacios et al., 2013). Soil organisms are supposed to sensitively adapt to the changed climatic conditions through shifts in their biotic activity, and through changes in their community structure and function (Keiser and Bradford, 2017). We suggest that soil microbes and soil fauna might play different roles in climate-induced changes of litter decomposition dynamics under different circumstances and propose this as a working hypothesis for future studies.

Litter decomposition is not only controlled by climate, but also by land use through altered decomposer communities, and therefore an interacting effect between both global change drivers on litter decomposition can be expected (Walter et al., 2013). Land-use intensification is supposed as the most immediate and widespread global change driver, with potentially significant consequences for litter decomposition (Bakker et al., 2011). An extensive management with greater inputs of complex organic matter is suggested favoring fungal-based energy channels and the contribution of arthropods in contrast to rather bacteria-based channels under intensive management (Bardgett et al., 2005). Consequently, the density and diversity of both soil fauna and microbiota have been found to be decreased with the conversion of grasslands to croplands (French et al., 2017; Mäder et al., 2008; Mulder et al., 2011; Stamou et al., 2011) as well as with the increased management intensity within these land-use types (Siepel and Van de Bund, 1988; Tsiafouli et al., 2015). In contrast to all of these findings, we found higher decomposition rates in croplands than in grasslands and no differences between management intensities within these two land-use types. Moreover, the overall contribution of soil fauna to litter decomposition was higher in croplands compared to grasslands, whilst microbial-driven decomposition was similar between the two land-use types. However, the assessment of macro- and mesofauna in this experiment revealed higher abundances in the grasslands (Yin et al., submitted), whilst climate had only minor effects on certain taxa. The underlying mechanisms remain unclear, which is why we can only provide hypotheses for subsequent studies.

The “home-field advantage” has often been applied to explain the adaptation of soil organisms to the local plant material (Gholz et al., 2000; Austin et al., 2014). Thus, adaptation of soil organisms and the associated “home-field advantage” may also explain the faster decomposition of oat litter in this study. However, in our experiment, oat was planted as homogenizing crop on all plots (croplands and grasslands) in 2013 before the start of the experiment, and in the year before our experiment started (2014), no cereals were grown in the both cropland regimes, providing limited support for this assumption. We therefore suggest that the microclimatic conditions in the croplands were more favorable (with more shade and higher humidity) for soil faunal activities due to the higher aboveground vegetation compared to grasslands.

Taken together, the present assessment of decomposition rates across two years and five land-use types indicates that predicted climate change with slightly higher temperatures and shifts in precipitation patterns will decelerate decomposition of organic material by reducing the contribution of soil fauna to this process. In contrast to our expectation, climate treatment and land use showed no interacting effects on decomposition rate. Thus, the negative influence of future climate was consistent across the two land-use types as well as across the intensity gradients within the land-use types. Both, land use and climate, affect leaf traits which determine the decomposability of litter produced by plants and plant communities (Fortunel et al., 2009). The results of Walter et al. (2013) suggest that management induced changes of litter quality importantly contribute to land-use specific effects of climate change on decomposition. As we used a standard material as litter in our study, we ignore the indirect effects of global change on litter quality and focus on the direct effects on the processes which determine decomposition dynamics. Future studies should investigate the main drivers of detritivore effects, the role of litter quality, and mitigation strategies to support a more active decomposer community in a changing world.

Conflicts of interest

The authors declare no conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.soilbio.2019.01.009>.

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